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Nitrogen mineralization in upland Precambrian Shield catchments: Contrasting the role of lichen-covered bedrock and forested areas

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Abstract. The upland boreal forest at the Experimental Lakes Area (northwestern Ontario, Canada) is characterized by treed soil islands interspersed within lichen and moss-covered bedrock outcrops. N mineralization was 2.5-fold and net nitrification was 13-fold higher on an areal basis over bedrock surfaces because of high mineralization rates under lichen and moss patches. The higher average soil temperature in lichen and moss patches could not account for the difference in mineralization rates. Lichens did not provide a significant additional source of N because they did not fix atmospheric N. A refractory conifer litter with a high C:N probably favours the immobilization of N in forest islands. Buried bag and *in situ* core incubations yielded similar net N mineralization rates but core incubations underestimated net nitrification rates. Both methods did not adequately measure dissolved organic N (DON) production rates because soil disturbance caused high initial DON concentrations. The higher export of mineral N from bedrock surfaces is probably a combination of the lower retention of N in precipitation and leaching of mineralized N from lichen and moss patches.

Introduction

In the boreal forest, nitrogen is often a limiting nutrient for plant growth because low soil temperature, low soil pH, and refractory litters limit N-recycling through mineralization of the forest floor (Van Cleve & Yarie 1986; Bonan & Shugart 1989; Van Cleve et al. 1990). Frequently, nutrient storage and primary production are higher in the lichen and moss mats covering the forest floor than in trees (Rencz & Auclair 1978; Oechel & Van Cleve 1986). Lichen and moss mats are generally thought to promote nutrient deficiency in trees by successfully competing for nutrient inputs in rain, by generating refractory litter, and by cooling the forest floor (Oechel & Van Cleve 1986).

However, it is possible that lichen and moss mats are not always a strong sink for nutrients. Upland Precambrian Shield catchments at the Experimental Lakes Area are a mozaic of forest islands interspersed within lichen and moss-covered bedrock outcrops (Figure 1). Allan et al. (1993) have demonstrated

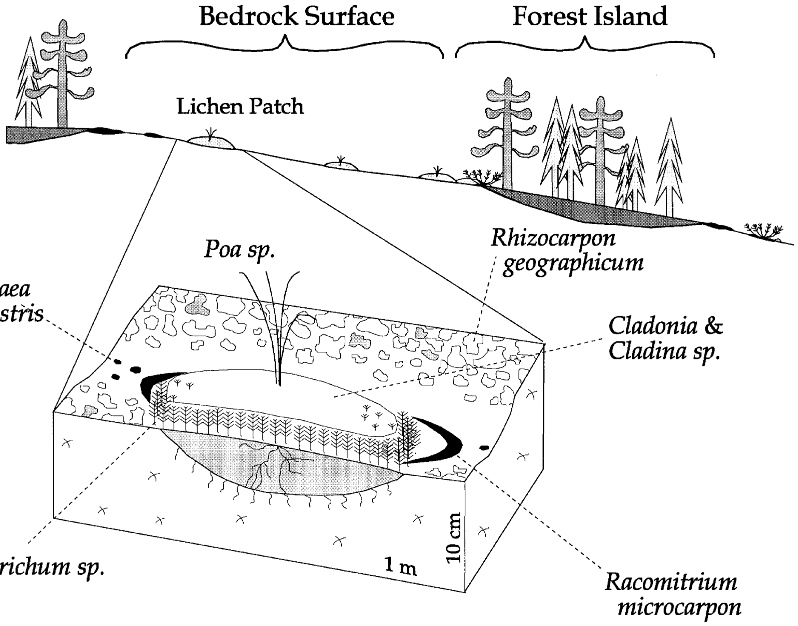

Figure 1. Cross-section of the Upland boreal forest landscape at the Experimental Lakes Area, northwestern Ontario. Jack pine and black spruce occur in forest islands with soils 10 to 50 cm deep. Deposits between 1 to 10 cm thick are found under lichen patches. On topographic highs, exposed bedrock often covers 70% of the landscape in this region.

that while forest islands and bedrock surfaces exported similar quantities of dissolved organic N (DON), mineral N retention was larger in forest islands. Allan et al. (1993) hypothesized that the higher mineral N export from bedrock surfaces was caused by fast hydrological flushing limiting the retention of N in precipitation and N fixation by lichen providing a source of mineralizable N. Alternatively, N mineralization may be higher under lichen and moss patches because of a different composition of soil organic matter (Nadelhoffer et al. 1991), warmer and drier conditions (Van Cleve & Yarie 1986), and a low immobilization of mineral N through root uptake (Johnson 1992).

As a part of a whole-catchment study of N-cycling, net mineralization ($\mathrm{MIN}_{\mathrm{net}}$) and net nitrification rates ($\mathrm{NO}_3^-{}_{\mathrm{net}}$) were measured in forest islands and lichen patches of an upland boreal forest. The main objective was to determine whether there were differences in N mineralization rates on a seasonnal and annual basis between lichen patches and forest islands. In addition, the potential for warmer soil temperature and lichen N fixation to promote higher mineralization rates in lichen patches was tested. Mineralization rates were estimated using buried bag incubations (Eno 1960) and validated with two experiments. First, the buried bag assay was compared to *in situ* core incubations (Raison et al. 1987), another common method used to estimate field N mineralization. Second, the assumption of the linearity of mineralization rates during incubations was tested in both soil types (Adams et al. 1989). The latter experiment also explored the possibility of measuring DON production rates from buried bag incubations.

Methods

Site description

All experiments were performed in the upland catchments of the Experimental Lakes Area, a set of small watersheds used to study processes controlling element export to shield lakes (Allan et al. 1993; Allan & Roulet 1994a, b; Allan 1995). Climate at the ELA is humid continental, with a mean average temperature of 2.3 °C and a mean annual precipitation of 673 mm (27% of which occurs as snow; Beaty & Lyng 1989). Soils at the ELA are thin and classified as truncated orthic humic regosols and sombric brunisols (Canadian Soil Survey Committee 1978; Allan & Roulet 1994a). Mineral soils within the Upland catchments fall in the silt loam size-range and are probably of eolian origin. Bedrock is mostly slow weathering pink granodiorite (McCullough & Campbell 1993). Wildfires are frequent in the area (Bayley et al. 1992) and the last fire in the Upland catchments occurred approximately 120 years ago.

The distribution of vegetation within the catchments is heterogeneous but follows a characteristic pattern (Figure 1). Trees occur in small depressions with 10 to 50 cm of organic and mineral soil (approximately 30% of catchment area). Jack pine (*Pinus banksiana* Lamb.) is common on the thinner soil while black spruce (*Picea mariana* Mill. B.S.P.) and a few white pine (*Pinus strobus* L.) occur where soils are deeper. Most trees were probably regenerated following the last wildfire. Currently, the fall of senescent Jack pine creates openings that are colonized by pin cherry (*Prunus pensylvanica* L.f.), red maple (*Acer rubrum* L.) and black spruce, the latter through vegetative growth. The understory comprises the shrub *Juniper communis* L., the lichen *Cladinia mitis* (Sandst.) Hustich and the moss *Pleurozium schreberi* (Brid.) Mitt. The forest floor is 5 to 25 cm thick and composed of L, F, and H horizons. Locally, a S horizon composed of undecayed moss stems is present. The mineral soil is 10 to 40 cm thick and limited to one to several A_h horizons, and occasionally a C or Cg horizon (Allan et al. 1993; Allan & Roulet 1994a).

Bedrock outcrops cover approximately 70% of the catchments and are composed of two features (Figure 1). About 65% of the bedrock outcrops is covered with crustose lichen such as *Rhizocarpon geographicum* (L.) DC. and some foliose lichen. The remaining bedrock surface is covered by clumps of the fruticose lichens *Cladina* spp. and *Cladonia* spp., the mosses *Polytrichum.* spp., *Andreaea rupestris* Hedw.and *Racomitrium microcarpon* (Hedw.), some herbs and grasses, and the shrub *Juniper communis* (L.) These organisms occur together in well-stratified units – hereafter referred to as lichen patches for simplicity (Figure 1). One to 10 cm deposits are found under lichen patches (nonsoil under the Canadian Soil Survey Committee 1978). In general, lichen patch 'nonsoil' can be divided into a S horizon of standing, undecayed moss stems and grasses, an L horizon of flattened and slightly decomposed mosses, lichens and grasses, and a mineral-rich H or A_h horizon ('H' hereafter). Lichens are predominant in upslope areas while mosses are more common in seepage areas downslope from forest islands (Vitt 1991). The diameter of lichen patches ranges from 30 cm to 3 m. Based on the lateral growth rate of *R. microcarpon* moss colonies, Vitt (1991) estimated that extant moss colonies could date from as far back as the last fire.

Monthly N mineralization assay

Three-week buried bag incubations where carried in May to October 1995 and 1996 in catchment U1. Ten forest floor stations and five lichen patches were monitored in 1995, and eight stations in each soil type in 1996. Soil cores were collected using a 2 cm dia. steel soil corer. Soil cores for initial extractable N concentrations were kept at 4 °C until processing (usually within 24 h). Incubated soil cores were placed into polyethylene bags (Nasco Whirl-Packs 7.5 × 16 cm for cores shorter than 10 cm and 11 × 21 cm for longer cores), sealed tightly, and returned to the soil. In forested areas, most cores collected were 15 cm or shorter. When longer cores were obtained, only the top 15 cm portion was retained. At most sites, this would encompass the LFH organic layer and the upper part of the A_h mineral horizon. When present, the S horizon was excluded. Soil cores obtained in lichen patches were 2.5 to 7 cm long and included the complete profile with the exception of the S horizon. Soil temperature was monitored weekly at mid-day at 5 cm depth in two lichen patches and two forest islands.

The effect of location on N mineralization rates was tested with a reciprocal transplant experiment in May 1996, a period when the temperature difference between the forest floor and lichen patches is maximum. Eight lichen patch and forest floor soil bags were transplanted. This experiment was run concurrently with the monthly N mineralization assay.

Validation of buried bag incubations

In July and August 1994, buried bag N mineralization estimates in forest islands were compared to *in situ* core incubation estimates (Raison et al.

1987). For *in situ* core incubations, one core for initial N concentration was taken at each sampling station. Two additional cores were inserted in the soil, one open to the atmosphere and the other covered with a plastic film. At the end of the incubation, a final core was taken. The rational behind the *in situ* core incubation is that the open core monitors mineralization minus leaching losses, the covered one measures mineralization without leaching losses, and the final core estimates mineralization minus leaching losses and minus plant uptake (Raison et al. 1987). For *in situ* core incubations, cores were made of PVC (5.2 cm dia. × 17 cm long) and buried to a depth of 15 cm. Twelve buried bags and ten sets of cores were incubated in both catchment U1 and in nearby U3 for 28 days. Upon retrieval, soil in the PVC cores was extruded by 5 cm intervals and analyzed separately. To reduce the labour involved, sets of PVC cores were pooled to give six replicates. In June and July 1996, the linearity of mineralization rates obtained with buried bags was tested in both soil types. Twenty-eight bags were placed in a 5 m^2 area of forest floor and in a 2 m^2 lichen patch. Four bags were retrieved from each area after 0, 1, 2, 3, 4, 6 and 8 weeks.

N fixation by lichen

Lichen N-fixation was estimated using acetylene-reduction incubations and by comparing the ^{15}N signature of lichen to the one of non N-fixing plants. For acetylene reduction assays, six ca. 10 g wet weight composite *Cladina* and *Cladonia* lichen samples were incubated on three occasions in May and June 1995. Samples were placed in 160 mL serum bottles and capped. Ten percent of the headspace was replaced with acetylene. Bottles were incubated in the shade to prevent overheating. Ten mL gas samples were collected after 1, 8 and 24 hours using the double-syringe technique and stored in evacuated 10 mL blood serum tubes. Lichen samples free of acetylene and air blanks were included with all incubations. On one occasion with dry antecedent conditions, triplicate lichen samples were soaked in local runoff water for an hour prior to the incubation. Acetylene and ethylene concentrations were determined by flame ionization detection using a Hewlett-Packard model 5750 gas chromatograph at the Freshwater Institute, Winnipeg, Manitoba (detection limit 0.02 $\mu M\ C_2H_2\ L^{-1}$).

N-fixers tend to have a ^{15}N signature closer to atmospheric N_2 ($\delta^{15}N$ = 0‰) compared to non-N-fixing plants (Peterson & Fry 1987). Six composite samples of the lichen *Cladina mitis*, and the mosses *R. microcarpon* and *Polytrichum* spp. were collected in August 1994. *Cladina mitis* and *Polytrichum* spp. occur on top of the patches and presumably obtain most of their N from precipitation. *Racomitrium microcarpon* is a creeping moss and probably receives N from precipitation and seepage from lichen patches. Moss and lichen samples were freeze-dried, and ball milled. Isotopic ratios were determined using a VG continuous flow mass-spectrometer connected to a Carlos Erba elemental analyzer at the University of Waterloo Environmental Isotope Laboratory.

Analytical procedures for extractable soil N

Soil samples were kept at 4 °C in the dark until extraction and analysis (usually within 24 h of collection). Cores were weighed and live plants, large roots, twigs and gravel were removed by hand. The soil was then thoroughly homogenized. Five g sub-samples were collected for water content determination and for N extraction. Soil water content was determined gravimetricaly by drying for 24 hours at 60 °C. Soil moisture content was expressed relative to the saturated water content of the soil, determined by letting thoroughly wetted soil sub-samples drain on a filter paper for 12 hours. N was extracted by shaking the soil sub-sample vigorously for 1 h in 50 mL 2M KCl. The soil extracts were pre-filtered on combusted and washed Whatman GF/C filter and filtered on combusted and washed Whatman GF/F filter (nominal pore size 0.7 μm). The extracts were stored in tightly sealed glass vials at 4 °C until analysis.

Total dissolved N, NH_4^+ and NO_3^-/NO_2^- concentrations were determined colorimetricaly following a procedure modified from Stainton et al. (1977). Nitrite concentrations were always low to non-detectable and were pooled with NO_3^- concentrations. Dissolved organic N was estimated as TDN (by UV-persulphate digestion) minus NH_4^+ and NO_3^- concentrations. Brine extracts were diluted at least 10X with distilled deionized water prior to TDN analysis. Volumetric N concentrations were converted to ug N per g soil dry weight, and then to g N ha^{-1} by multiplying by the average dry mass of the initial and final cores divided by the core area.

Only net rates of mineralization can be measured with the incubation techniques used (Nadelhoffer et al. 1984; Stark & Hart 1997). Net nitrification ($NO^-_{3\ \mathrm{net}}$) was estimated as the change in NO_3^- concentration (or areal mass) over time and net mineralization (MIN_{net}) as the change in $NH_4^+ + NO_3^-$ over time. An added complication when estimating DON production rates is determining the proportion of mineralized N originating from particulate N or DON (Eviner & Chapin 1997). A high DON production estimate (DON_{max}) can be made by assuming all mineral-N produced originates from DON, and a low estimate (DON_{min}) by assuming all mineral-N originates from particulate N. Errors on monthly mineralization rates were calculated using first-order error propagation, assuming no covariance between terms (Meyer 1975). Annual net mineralization budgets were calculated by summing monthly mineralization estimates.

Table 1. Forest island and lichen patch organic soil characteristics. Replicates (*n* = 4) were obtained by pooling samples from several stations in each soil type (*n* = 8 for lichen patch %C and %N). Soil pH was obtained by mixing 5 g of homogenized, 2 mm sieved, dried soil to 10 mL of distilled water or 0.1M $CaCl_2$. Mean ± SE. Volume weighed runoff pH from Allan et al. (1993). Carbon to N ratios are expressed on a molar basis.

L & 'H'	Lichen patches LFH	Forest islands
pH (H_2O)	4.38 ± 0.14	4.08 ± 0.13
pH (0.1M $CaCl_2$)	3.86 ± 0.15	3.55 ± 0.12
Volume weighed runoff pH	4.66	4.01
%C	15 ± 3.0	31 ± 6.0
%N	0.86 ± 0.16	1.0 ± 0.2
C:N	15	27

Results

Validation of the buried bag assay

During the 8-week period where one site of each soil type was intensively sampled, mineralization rates were roughly linear for mineral-N species but not for DON (Figure 2). In lichen patches, there was a large accumulation of NO_3^- over time but little net change in NH_4^+ concentration. Net mineralization rates in the forest island site were lower than in the lichen patch site, with only NH_4^+ concentration having a significant increase over time (Figure 2 & Table 2). A spike in DON occurred in both soil types at the beginning of incubations, probably due to disturbance and root cutoff during core collection (Hendrickson & Robinson 1984; Clarholm et al. 1981). Most of the excess DON appears to have been consumed after one week of incubation, and DON concentrations tended to increase thereafter (Figure 2). Qualitative estimates of DON production were calculated using DON concentration *after one week of incubation* as the initial concentration (Table 2). Dissolved organic nitrogen production (as DON_{max}) was 2-fold higher than MIN_{net} in the lichen patch site, and 2.5-fold MIN_{net} in the forest island site. Dissolved organic nitrogen production rates in the other experiments could not be corrected for a potential initial DON spike, therefore they will not be presented here.

Net mineralization rates were not significantly different between *in-situ* cores and buried bags (MIN_{net}: 105 vs 89 g N ha^{-1} d^{-1} respectively; Table 3) However, $NO_{3\ net}^-$ was significantly lower in cores when rates are expressed on an areal basis (-3.8 vs 1.9 g N ha^{-1} d^{-1}; Table 3). Leaching of NO_3^- from both open and covered cores probably occurred when the water table

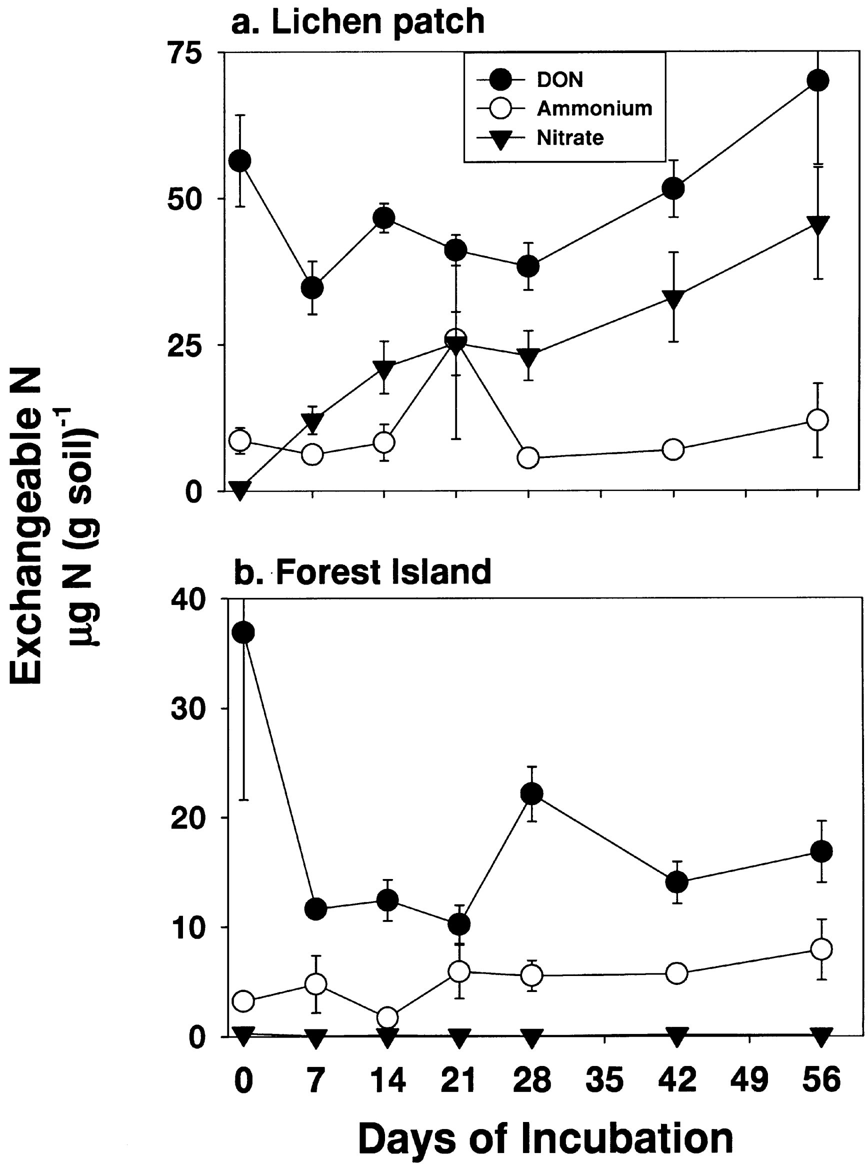

Figure 2. Change in DON, NH_4^+, and NO_3^- concentrations in buried bags incubated in one intensively sampled **a)** lichen patch and **b)** forest island site in June and July 1996. Weekly, mid-day, soil temperature varied in a non-systematic fashion between 16 to 21 °C in the lichen patch and 13 to 17 °C in the forest island.

Table 2. Average mineralization rates over an 8-week period in one intensively sampled forest island and one lichen patch in June–July 1996. Organic matter content estimated from loss on ignition. Mineralization rates were assumed linear as a first approximation and were estimated using least-square regression. Dissolved organic nitrogen production estimates were calculated using the concentration of DON after one week of incubation as the initial concentration.

	DON_{min}	DON_{max}	MIN_{net}	$NO_{3\ net}^{-}$
		$\mu g\ N\ g^{-1}\ d^{-1}$		
Lichen patch	0.61^{*}	1.3^{*}	0.73^{*}	0.70^{*}
Forest island	0.11	0.18	0.078^{*}	0
		$\mu g\ N\ g$ organic matter$^{-1}\ d^{-1}$		
Lichen patch	1.3	2.5	1.4^{*}	1.4^{*}
Forest island	0.11	0.21	0.093	-0.002
		$g\ N\ ha^{-1}\ d^{-1}$		
Lichen patch	165^{*}	331^{*}	166^{*}	167^{*}
Forest island	72	114	42^{*}	-1.4

* slope significantly different from 0 ($P < 0.05$)

rose to the surface in low-lying areas during large storms (Lamontagne pers. obs.) Consequently, it was not possible to estimate leaching losses using the difference in N concentration between covered and open cores (not significantly different than 0 for both MIN_{net} or $NO_{3\ net}^{-}$; $P > 0.05$). Therefore, the ‘plant uptake’ term (covered – final core) represent both plant uptake and leaching losses during incubations (Table 3). The loss of mineral N through runoff is very small in forest islands (ca. 0.02 kg N ha^{-1} yr^{-1}; Allan et al. 1993), therefore the plant uptake terms are probably accurate. The amount of mineral N produced through mineralization was similar to plant uptake during the incubation (Table 3). Most of the N mineralization occurred in the top 10 cm of the forest island soil profile (Table 3).

Lichen patch and forest island N mineralization

On an annual basis, MIN_{net} was 7-fold and $NO_{3\ net}^{-}$ 40-fold higher in lichen patches than forest islands (Figure 3). In forest islands, peak MIN_{net} occurred in June and July, while significant $NO_{3\ net}^{-}$ was only measured in August ’95 when soil moisture was low. In lichen patches, peak MIN_{net} occurred in June and peak $NO_{3\ net}^{-}$ in July and August (Figure 3). Overall, lichen patches were only sligthly warmer than forest islands. The average May to October soil temperature at 5 cm was 11.6±4.0 °C in the forest islands

Table 3. Nitrogen mineralization estimates obtained with buried bag and *in situ* core incubations in July-August 1994 in forest islands. In the *in situ* core incubation, the plant uptake term also includes leaching losses because the latter could not be accurately estimated. Total mineralization estimates in cores are weighed by the average soil mass in the core section when expressed on a per gram of soil basis, and added between section when expressed on an areal basis. Total mineralization estimates obtained with both buried bags and cores are not significantly different (t-tests), except for $\mathrm{NO}_{3\ \mathrm{net}}^{-}$ when expressed on an areal basis ($P < 0.05$).

a) $\mathrm{MIN}_{\mathrm{net}}$

		μg N (g soil)$^{-1}$ d^{-1}		g N ha^{-1} d^{-1}	
Method	Depth	$\mathrm{MIN}_{\mathrm{net}}$	Plant uptake	$\mathrm{MIN}_{\mathrm{net}}$	Plant uptake
Core	0–5 cm	0.33 ± 0.18	0.40 ± 0.15	57 ± 33	68 ± 32
	5–10 cm	0.14 ± 0.07	0.14 ± 0.08	41 ± 21	41 ± 20
	10–15 cm	0.02 ± 0.013	0.04 ± 0.02	7.3 ± 3.1	13 ± 7
	Total	0.12 ± 0.08	0.14 ± 0.08	105 ± 39	121 ± 39
Bag	Total	0.21 ± 0.07		89 ± 24	

b) $\mathrm{NO}_{3\ \mathrm{net}}^{-}$

		μg N (g soil)$^{-1}$ d^{-1}		g N ha^{-1} d^{-1}	
Method	Depth	$\mathrm{NO}_{3\ \mathrm{net}}^{-}$	Plant uptake	$\mathrm{NO}_{3\ \mathrm{net}}^{-}$	Plant uptake
Core	0–5 cm	−0.02 ± 0.004	−0.001 ± 0.003	−2.02 ± 0.49	−0.13 ± 0.09
	5–10 cm	−0.002 ± 0.006	0.003 ± 0.003	−0.654 ± 1.6	0.60 ± 0.75
	10–15 cm	−0.004 ± 0.014	0.002 ± 0.003	−1.1 ± 2.3	0.78 ± 0.65
	Total	−0.005 ± 0.006	0.002 ± 0.003	−3.8 ± 2.8	1.25 ± 1.0
Bag	Total	0.004 ± 0.002		1.9 ± 0.9	

and 15.4±4.7 °C in lichen patches. Temperature differences were largest during spring and summer, and smallest in fall (Figure 3). Geothermal heat exchange with bedrock probably moderates the influence of declining average air temperature and lower solar insolation in fall. Both soils were usually unsaturated during summer months (Figure 3).

In lichen patches, monthly $\mathrm{MIN}_{\mathrm{net}}$ and $\mathrm{NO}_{3\ \mathrm{net}}^{-}$ were positively related to cumulative degree-days above 0 °C during incubations (r = 0.61, $P < 0.05$ and r = 0.84, $P < 0.001$ respectively), but were weakly correlated to relative saturation ($r = -0.34$, $P > 0.05$; $r = -0.48$, $P > 0.05$). Monthly forest floor mineralization rates were poorly correlated to both cumulative degree-days and relative saturation. During the reciprocal transplant experiment, the average soil temperature was 3.4 °C in forest islands and 8.1 °C in lichen patches.

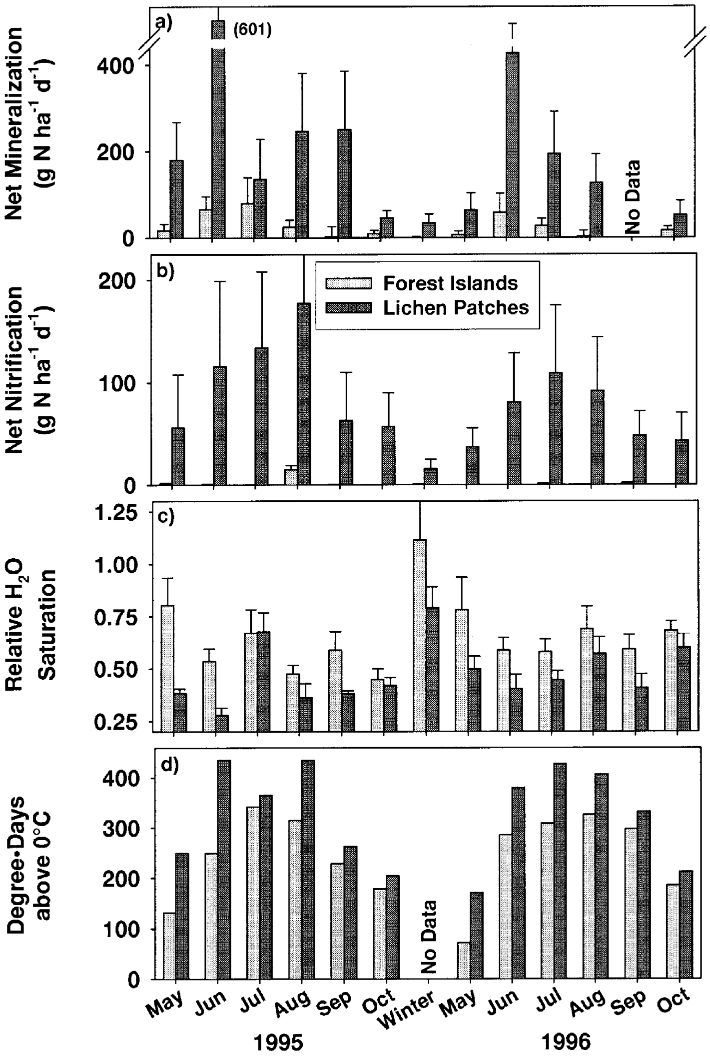

Figure 3. Average monthly **a**) MIN_{net}, **b**) $NO_3^-{}_{net}$, **c**) relative soil moisture content of initial bags, and **d**) cumulative degree-days above 0 °C (during the 21 days of incubation) for catchment U1 in 1995–1996.

Transplanted soil from lichen patches behaved similarly to controls (Table 4). The comparison of mineralization rates between control and transplanted forest island soil was inconclusive because rates were very low and variable (Table 4).

Table 4. Buried bag mineralization rates (in g N ha^{-1} d^{-1}) for forest floor and lichen patch soil incubated in their location of origin and transplanted in the other area in May 1996. Mean ± 1 SE, n = 8, ns = $P > 0.05$.

	Control	Transplant	*t*-test
	Lic → Lic	*Lic → For*	
MIN_{net}	65 ± 39	83 ± 44	0.1^{ns}
$\text{NO}_3^-{}_{\text{net}}$	37 ± 19	49 ± 33	0.09^{ns}
	For → For	*For → Lic*	
MIN_{net}	7 ± 9	2 ± 18	0.06^{ns}
$\text{NO}_3^-{}_{\text{net}}$	0 ± 0	0.1 ± 0.1	1.0^{ns}

Lichen N fixation

No N-fixation by desiccated or moist lichen was detected during acetylene-reduction incubations (data not shown). The absence of ethylene was verified by adding small amounts to samples (Len Hendzel, Freshwater Institute, Winnipeg, Manitoba, pers. comm.) The lichen *Cladina mitis* was more depleted in ^{15}N (δ^{15}N = −4.08 ± 0.40‰; mean ± SE) than the mosses *Polytrichum* spp. and *R. microcarpon* (−1.70 ± 0.24‰ and −3.4 ± 0.5‰ respectively). Thus, N-fixation by lichen is not an important source of N in this system.

Discussion

Differences in soil organic matter composition are probably more important than temperature in generating the patterns in N mineralization between forest islands and lichen patches. In laboratory incubations of six tundra soils, Nadelhoffer et al. (1991) found that the composition of soil organic matter was more important than soil temperature in controlling rates of N mineralization, especially at temperature below 9 °C. Similarly, Hobbie (1996) suggested changes in vegetation community structure brought by future warming in the tundra may have a stronger influence on N recycling rates than changes in soil temperature.

Forest island N mineralization

Either low gross mineralization rates or strong immobilization of mineral N can account for low MIN_{net} and $\text{NO}_3^-{}_{\text{net}}$ in forest islands. The C:N of the soil organic matter in forest islands is high (27), which should favour the immobilization of mineral N by microorganisms (Janssen 1996). On the other hand, conifer litter from acidic and nutrient-poor sites tends to be enriched in compounds refractory to mineralization such as polyphenols (Davies 1971; Northup et al. 1995). The low availability of labile C has also been shown to limit decomposition rates in *P. banksiana* litter (Foster et al. 1980). Although soil pH (4.08) was lower in forest islands, it was probably not low enough to prevent autotrophic nitrification (Tietema et al. 1992; Persson & Wirén 1995). Denitrification may have also lower $\mathrm{MIN}_{\mathrm{net}}$ by removing NO_3^- from soil solution. However, under pristine conditions, denitrification tends to be low in boreal forests and wetlands because of rapid removal of NO_3^- from soil solution by plants and microorganism (Bowden 1987; Urban et al. 1988; Blew & Parkinson 1993). Net N mineralization in forest islands is low when compared to Alaskan conifer forests ($\mathrm{MIN}_{\mathrm{net}}$12-20 kg N ha^{-1} yr^{-1}; Van Cleve et al. 1983; Van Cleve & Yarie 1986), although comparisons are difficult as methodology varies greatly between studies.

Lichen patch N mineralization

Higher $\mathrm{MIN}_{\mathrm{net}}$ and $\mathrm{NO}_{3\ \mathrm{net}}^-$ in lichen patches is consistent with a lower potential for N immobilization because of the low C:N (15) of the soil organic matter. Although moss and lichen litter decomposes slowly (Heal & French 1974; Moore 1981), rates can increase when the litter is exposed to wetting and drying cycles (Chapin et al. 1988; Belyea 1996). Lichen patches have rapid and frequent wetting and drying cycles because of the absence of canopy interception of precipitation, low water storage capacity, and lateral flow of runoff over bedrock surfaces (Allan & Roulet 1994b). The presence of fast-decomposing graminoid litter (Hobbie 1996) and higher exposure to visible and UV-light (Gehrke et al. 1995) may also increase mineralization rates in lichen patches. Net N-mineralization in lichen patches is of similar magnitude as $\mathrm{MIN}_{\mathrm{net}}$ in boreal wetlands. However, $\mathrm{NO}_{3\ \mathrm{net}}^-$ is usually nil in the latter ecosystem (Urban & Eisenreich 1988; Bowden 1987).

N fixation

N fixation by lichens is not a significant source of N to lichen patches. The most abundant lichen species (*Cladina* and *Cladonia* spp.) are not strong N-fixers (Millbank 1976; Alexander & Billington 1986). On the other hand, N fixation by free-living cyanobacteria associated with mosses has been shown to be more important than lichen N fixation in the Alaskan taiga (Alexander & Billington 1986). The ^{15}N signature of the mosses *Polytrichum* spp. and *R. microcarpon* was closer to atmospheric N than the lichen *C. mitis*, suggesting that N-fixation may be a source of N to moss growth in lichen patches. The

Table 5. Contribution of different landscape units to annual net N mineralization budgets in catchment U1 for 1995 and 1996. Forest islands cover 27%, lichen patches 24%, and bedrock with only crustose lichen 49% of catchment area. 'Bedrock surfaces' is the combination of lichen patches and crustose lichen-covered bedrock. It was assumed that N mineralization is nil over crustose lichen-covered bedrock areas. Overwinter bags were only incubated in the winter of 1995–96 but were used in the annual budget calculations for both years.

Year	MIN_{net}	NO_3^- net
	kg N (ha of unit)$^{-1}$ yr^{-1}	
	Lichen Patches	
1995	50 ± 12	21 ± 5
1996	33 ± 7	15 ± 3
	Bedrock Surfaces	
1995	16 ± 4	6.9 ± 1.6
1996	8.9 ± 2.0	4.9 ± 1.0
	Forest Islands	
1995	6.3 ± 2.3	0.45 ± 0.18
1996	3.9 ± 1.6	0.01 ± 0.10
	Catchment U1	
1995	13 (90%)*	5.2 (97%)
1996	7.6 (85%)	3.6 (99%)

* Percent contribution from lichen patches

moss *P. schreberi* is common in forest islands and has also been shown to have N-fixing activity (Alexander & Billington 1986). Thus, moss-associated N fixation may represent a significant input of N in both lichen patches and forest islands.

Bedrock surfaces and forest islands contribution to catchment N export

Despite small biomass and soil volume, bedrock surfaces account for 87% of net N mineralized on a yearly basis in the upland catchments (Table 5). Patterns in N mineralization are in agreement with N export through runoff from bedrock surfaces and forest islands. Allan et al. (1993) showed that bedrock surfaces export more NO_3^-, NH_4^+, and particulate N than forest islands. Higher N export from bedrock surfaces is probably a combination of lower retention of N input in precipitation and leaching of mineralized N from lichen patches. Thus, upslope bedrock surfaces are a source of N to forest islands, and forest islands are better at N retention than estimated from atmospheric input alone because of the downslope translocation of nutrients.

In many areas of the Precambrian Shield, exposed bedrock can represent a significant proportion of lake perimeter. These areas are seldom gauged because they tend to occur on steep or unfocussed concave slopes. Because of higher water yields (Allan & Roulet 1994b) and lower immobilization of nutrients, neglecting the contribution of bedrock surfaces may underestimate nutrient load to shield lakes.

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